

THE DIGESTIVE TRACT OF CARASSIUS AURATUS

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INTRODUCTION

There have been many contributions, mainly morphological, to the knowledge of the structure of the alimentary tract of fishes. The most recent work¹ has been done by Babkin and Bowie (1928), Dawes (1929), Blake (1930, 1936) and Rogick (1931). An extensive review of the earlier literature is given by Dawes (1929) as well as by Blake (1930) and Rogick (1931).

While investigating the function of the alimentary canal in *Fundulus heteroclitus*, Babkin and Bowie (1928) found that it possessed no stomach nor any gland for the secretion of pepsin and hydrochloric acid. Accordingly, they studied the anatomy as well as the physiology of the tract in this species. They found that the first portion of the intestine joined directly to the oesophagus and was capable of dilating to form a container for food. Since the bile and pancreatic ducts entered this region of the gut, it was designated the duodenum. A sphincter between the oesophagus and intestine closely resembled in structure the pyloric sphincter of higher vertebrates.

In preparation for a physiological study of digestion in the plaice, Dawes (1929) investigated the histological aspects of its digestive tract. This species possesses a stomach with true digestive glands. The walls of all parts of the tract showed a similar fundamental plan in possessing mucous membrane, sub-mucous coat, inner circular and outer longitudinal muscle layers and a serosa. There was no evidence of either muscularis mucosae, stratum granulosum or stratum compactum. Consequently, the important variations in structure occurred in the mucous membrane and muscular layers of the separate regions. These were studied in considerable detail.

Blake, in 1930, presented a histological study of the gut of the sea-bass, *Centropristes striatus*. This fish, a predaceous teleost, was selected because of its feeding habits. For purposes of comparison, Blake

¹ Curry, E. 1939. The histology of the digestive tube of the carp (*Cyprinus carpio communis*). Abstract was received after completion of the work on *Carassius*.

studied later (1936) the digestive tract of the sea robin, *Prionotus carolinus*, a bottom-feeding form. He found the fundamental structure of the gut to be similar in both species. The oesophagus was a short tube leading into an elongated stomach. Pyloric caecae opened into the anterior end of the intestine. A distinct valve separated the intestine and rectum in *Centropristes* but could not be demonstrated in *Prionotus*.

Rogick (1931) investigated the microscopical anatomy of the entire tract of the minnow, *Campostoma anomalum* (Rafinesque). She found that the pharynx could be divided into an anterior and posterior region on the basis of characteristic structures present in each. The anterior part contained the visceral clefts. In the posterior portion were ventral pharyngeal teeth and a dorsal callous pad. A dorsal pocket and pneumatic duct characterized the short oesophagus. As in *Fundulus*, an enlargement of the intestine, the intestinal bulb, served as a container for food and represented that part of the gut normally occupied by the stomach. No gastric glands were found in this region. The intestine proper was of very simple type, lined with columnar epithelium and goblet cells.

The present paper includes a study of the gross and microscopical anatomy of the digestive tract of the goldfish, *Carassius auratus*. The investigation was begun at Yankton College at the suggestion of Dr. Austin P. Larrabee. At this time, it was found that *Carassius*, like *Fundulus* and *Campostoma*, does not possess a true stomach. It seemed desirable, therefore, to make a thorough histological study of the entire tract. In view of the absence of the stomach, it was of interest to determine whether glands of the gastric type could be found in any other part of the digestive tube. In this connection, the nature of the cells in the intestinal epithelium was also of importance. Consequently, the gross and microscopical anatomy of the posterior pharynx, oesophagus and intestine have been studied in detail.

MATERIAL AND METHODS

Both domesticated and wild goldfish were used. Of a total of sixteen individuals, four were studied for gross structure and twelve for microscopic. Both Helly's and Bouin's fixatives were employed. Transverse and longitudinal sections were made of the anterior portion of the tract. The intestine was cut transversely. Sections were mounted serially and successive slides were stained with Delafield's haematoxylin and eosin, Mallory's triple connective tissue stain, Heidenhain's iron alum haematoxylin and eosin, and mucicarmine.

GROSS ANATOMY

Table I shows the measurements for eight individuals. Total lengths included the distance from the tip of the snout to the end of the caudal fin. Measurements of the digestive tract as a whole were taken from the beginning of the posterior pharynx to the anus. It appears from these figures that the rather wide individual variations in length of the tract result chiefly from variations in length of the intestinal portion. In all cases, the digestive tube was considerably longer than the body cavity.

The posterior pharynx extended from the last gill arch to the beginning of the oesophagus. It appeared to be a more or less rigid organ; the bones of the ventral and lateral walls as well as the dorsal horny pad permitted very little stretching. It was wider at the anterior

TABLE I

Showing measurements of the body and of parts of the digestive tract in centimeters

Animal	Total length	Length of body cavity	Total length of tract	Posterior pharynx	Oesophagus	Intestine
A	12.0	5.0	40.0	0.8	0.3	38.9
B	13.0	4.5	19.0	0.5	0.2	18.3
D	12.0	4.5	29.95	0.6	0.25	29.1
E	15.0	5.0	35.0	0.7	0.3	34.0
F	12.0	4.0	30.5	0.6	0.3	29.6
H	11.0	4.0	23.45	0.6	0.25	22.6
I	13.5	4.8	32.0	0.8	0.3	30.9
J	12.6	4.5	29.92	0.65	0.27	29.0

end and narrowed gradually to its junction with the oesophagus. The anterior part did not lie free in the body cavity but was connected with the head musculature.

This portion of the pharynx contained the pharyngeal teeth. They were located laterally on a more or less horizontal line and slanted in a slightly dorsal direction. There were usually four teeth on each side attached to the inferior pharyngeal bones. The angle of their insertion permitted them to bite on the dorsal horny pad. The teeth were narrow, conical and lay with their flat sides closely against each other. The first tooth on each side was firmly joined to the bone while the rest of the teeth were more loosely attached. At the base of each tooth, and apparently attached to it where it joined the inferior pharyngeal bone, was an immature tooth.

The posterior pharynx was characterized also by the dorsal horny pad which lay at the junction of the two parts of the pharynx. It was

roughly triangular in shape, the wide end directed anteriorly. It had a median longitudinal ridge and, as a result, presented a more convenient biting surface for the teeth.

The oesophagus was a very short tube, averaging 0.3 cm. in length and 0.2 cm. in width. Both the anterior and posterior boundaries were clearly marked. From the dorsal surface extended a small diverticulum which connected with the second chamber of the air bladder.

The junction of oesophagus and intestine was marked by a circular constriction, the intestinal sphincter, and also by the sudden enlargement of the intestine to form the intestinal bulb. Although there was no sharp distinction, histologically, between this part and the intestine proper, a difference was evident both in relative size and in the complexity of the mucosal folds. The intestinal bulb was larger at its anterior end, quite straight, and narrowed gradually until it merged into the intestine proper. At its widest point its diameter was two or three times that of the rest of the intestine. The intestinal bulb was capable of great expansion. This was particularly evident in fish examined just after eating when the bulb was extended to about three times its original size. At such a time, the walls were so thin that the herringbone pattern of the mucosal folds could be clearly seen.

The intestine proper had a much smaller diameter than the intestinal bulb and was not capable of such great distension. The width was more or less uniform throughout, becoming slightly smaller as the anus was approached. The rectum, or terminal portion, was distinguished from the rest of the intestine by its straight course to the anus.

The intestine as a whole was greatly coiled. It was entirely separate from the air bladder and occupied the ventral portion of the body cavity. The method and direction of coiling followed the same general plan in all the fish studied, although individual details might differ. The first limb of the intestine, including the intestinal bulb and a small part of the intestine proper, extended without coiling to the posterior end of the body cavity. There, it turned sharply and continued anteriorly, usually toward the left side. From this point, the coiling showed individual variation. In general, however, it passed from the left to the right side and most of the coils were found on the right side. At some point in these coils on the right side, the intestine turned on itself and retraced the previous coilings. This continued until the terminal portion straightened out and became the rectum. When the intestine was uncoiled, this sharp bend appeared approximately in the middle of its length. The last part of the intestine was somewhat smaller and darkened with fecal matter but was, otherwise, not differentiated.

MICROSCOPIC ANATOMY

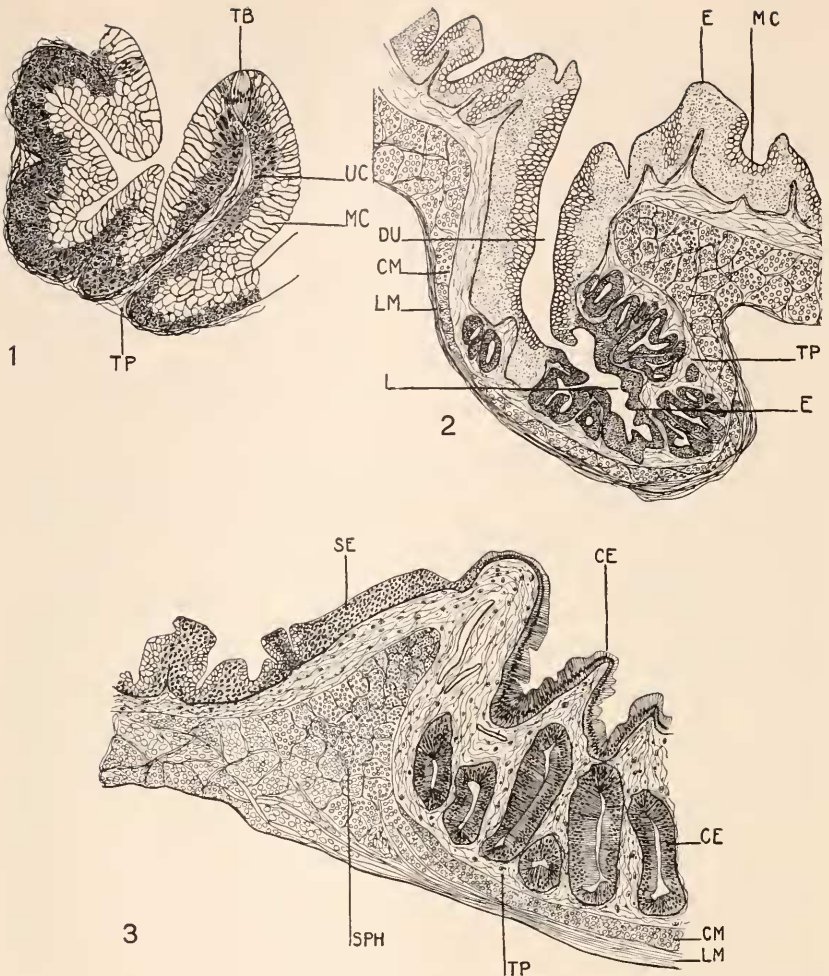
Pharynx

The mucous membrane of the posterior pharynx formed rather low, convoluted and branching folds. At the more anterior end, there appeared to be no regularity in arrangement but, toward the caudal end, these irregular folds became somewhat organized and continued into the longitudinal folds of the oesophagus. On the ventral surface, the folds were uniform in height producing the plateau-like appearance which Rogick (1931) found in the minnow. Near the pharyngeal teeth they were greatly elongated.

The wall of the pharynx consisted of three layers, the tunica mucosa composed of epithelium and sub-epithelial connective tissue, the tunica muscularis and the tunica serosa. These same three layers were found also throughout the rest of the tract. Absence of a muscularis mucosae in the digestive tract of fishes has led to certain departures from the commonly accepted terminology. Bridge (1910), in the Cambridge Natural History, designated the sub-epithelial tissue as submucosa; the mucosa, accordingly, comprised only the epithelium and basement membrane. Rogick (1931) followed this method in her description of the minnow. Blake (1930, 1936) and Scott and Kendall (1935), however, distinguished a tunica propria immediately below the epithelium which continued without interruption into the submucosa. Since this follows more closely the interpretation of comparable tissues in the higher vertebrates (Maximow-Bloom, 1938), the term "tunica propria" will be used throughout the present paper to indicate the connective tissue lying directly beneath the epithelium and forming the core of the mucosal folds.

The pharyngeal epithelium was apparently stratified columnar of a rather specialized type. The surface cells were greatly elongated mucous cells, closely packed, and resting on several layers of undifferentiated polyhedral cells (Fig. 1). These goblet cells were not so numerous at the tips of the mucosal folds and, in some cases, were entirely absent. They stained red with mucicarmine and showed a large-meshed cytoplasmic reticulum within the body of the cell.

A basement membrane could be distinguished although it was sometimes obscured by the dense connective tissue fibers immediately below it. These closely packed fibers stained intensely with Mallory's stain and were considered to be the stratum compactum. They formed a distinct layer in the posterior pharynx and could be identified in other parts of the tract as well. Rogick (1931) described a hyaline stratum compactum in the anterior pharynx but found no comparable structure in the posterior pharynx, oesophagus or intestine of the minnow. A



ABBREVIATIONS IN FIGURES

BC—Basophilic (mast) cells
CE—Columnar epithelium
CM—Circular muscle
DU—Duct
E—Epithelium
L—Lumen
LD—Liver duct
LM—Longitudinal muscle
M—Mesentery
MC—Mucous cells
N—Cells of myenteric plexus

P—Pancreas
PD—Pancreatic duct
S—Serosa
SC—Stratum compactum
SE—Stratified epithelium
SPH—Sphincter
TB—Taste bud
TP—Tunica propria
TPL—Top plate
UC—Undifferentiated cells
V—Vacuoles

FIG. 1. Longitudinal section of the mucosa of the posterior pharynx showing the stratified epithelium with mucous cells. Two taste buds are shown. $\times 80$.

FIG. 2. Semi-diagrammatic longitudinal section of the oesophageal diverticulum, showing its relation to the oesophagus. $\times 40$.

FIG. 3. Longitudinal section through the intestinal sphincter showing the transition from stratified epithelium of the oesophagus to simple columnar of the intestinal bulb. The sphincter marks the termination of the circular muscle of the oesophagus and the origin of the circular and longitudinal muscles of the intestine. $\times 40$.

layer of dense fibers which she found in the mouth and which she likewise considered the stratum compactum appeared similar in every way to the layer of dense connective tissue which was found throughout the digestive tract of *Carassius* and which Bolton (1933) observed in the trout and salmon.

Taste buds were present in the epithelium of the posterior pharynx. They were elongated and rather narrow. The cells extended from the basement membrane to a point just below the surface of the epithelium (Fig. 1).

The tunica propria of the pharynx contained many striated muscle fibers. Although they were chiefly longitudinal, some circular fibers were interwoven among them and they extended into the folds of the mucosa. Bolton (1933) found mast cells in the tunica propria of the digestive tract in several species of trout and salmon. His observations have been confirmed for *Carassius auratus* in the material which was fixed in Helly's solution.

There was no very sharp distinction between the tunica propria and tunica muscularis because of the muscle fibers which invaded the tunica propria. The muscular layer, itself, consisted of very heavy, striated circular fibers which were continuous with the circular muscle of the oesophagus.

Since the pharynx did not lie free in the body cavity, there was a serosa over the most posterior part only. It possessed the usual constituents, a thin layer of fibrous tissue covered by simple pavement epithelium.

Only a few imperfect sections of the functional pharyngeal teeth were obtained but their relation to the inferior pharyngeal bones could be determined. Longitudinal sections of the developing teeth presented much the same picture as that found in mammals. The primordium occupied a position in the thick muscular coat of the pharynx and was surrounded by connective tissue which was essentially the same as that of the tunica propria. The dentine was widest at the tip of the papilla and tapered down the sides to a very narrow line. It showed a faint but definite striation. On the outside of the dentine, closely applied to it, was a single layer of enamel cells. The odontoblasts, on the inner side of the dentine, were not so clearly defined as the enamel cells. The inner ends of the odontoblasts merged with the dental pulp.

Oesophagus

The tunica mucosa formed ten or twelve longitudinal folds which extended the length of the oesophagus. They were generally narrow at

the tip but were occasionally broadened so that in cross-section they had a mushroom-like appearance. In longitudinal section, this appeared as an invagination of the sides of the folds. Secondary or smaller folds occurred between the primary longitudinal folds.

All of the oesophageal folds were covered with a thick layer of stratified epithelium. The surface cells at the tips of the primary folds were characteristically flattened although this was not necessarily true of all folds. In some instances, the surface cells did not differ materially from those of the layers directly beneath. Cells of the deeper layers were often considerably elongated at right angles to the surface. Mucous cells were very numerous in the oesophagus as in the pharynx and presented, for the most part, the same appearance (Fig. 2). They extended only part way up the sides of the primary folds but entirely covered the smaller secondary folds. Nearer the intestine, they became fewer in number, occurring in the deep grooves between the folds and on the sides (Fig. 3). Where they were not closely packed, they were of the typical goblet-cell shape. The contents of the cells had a reticular appearance and gave the specific red color with mucicarmine.

The stratified epithelium of the oesophagus continued almost to the peak of the intestinal sphincter but ultimately gave way to a simple columnar type (Fig. 3). Here, the surface cells gradually disappeared and the basal layer continued over the sphincter as high columnar epithelium with darkly staining cytoplasm.

The tunica propria of the pharynx continued through the oesophagus with little change in appearance. It was difficult to make out a stratum compactum in the oesophagus but it was observed occasionally, especially when the section was stained with Mallory's stain. Where it could be distinguished, it appeared as a wavy line of one or two fibers directly below the basement membrane. The line of demarcation between tunica propria and tunica muscularis was difficult to determine because of invading muscle fibers. These longitudinal striated fibers were not arranged in layers and there appeared to be no fibers in that part of the tunica propria which extended over the sphincter.

The tunica muscularis itself consisted primarily of a thick layer of striated circular muscle with a few longitudinal fibers external to it. The fibers were bound into bundles by connective tissue continuous with that of the tunica propria and serosa. Although this muscle layer was narrower than that of the pharynx, it was much wider than that of the intestine.

At the junction of oesophagus and intestine, the circular muscle widened suddenly to approximately twice its original width and as abruptly narrowed again (Fig. 3). The muscle fibers were very large,

particularly at the periphery of the layer, and the entire band of circular muscle appeared to end at the termination of the sphincter. Small bands or isolated fibers of longitudinal muscle interrupted the continuity of the circular fibers at this point.

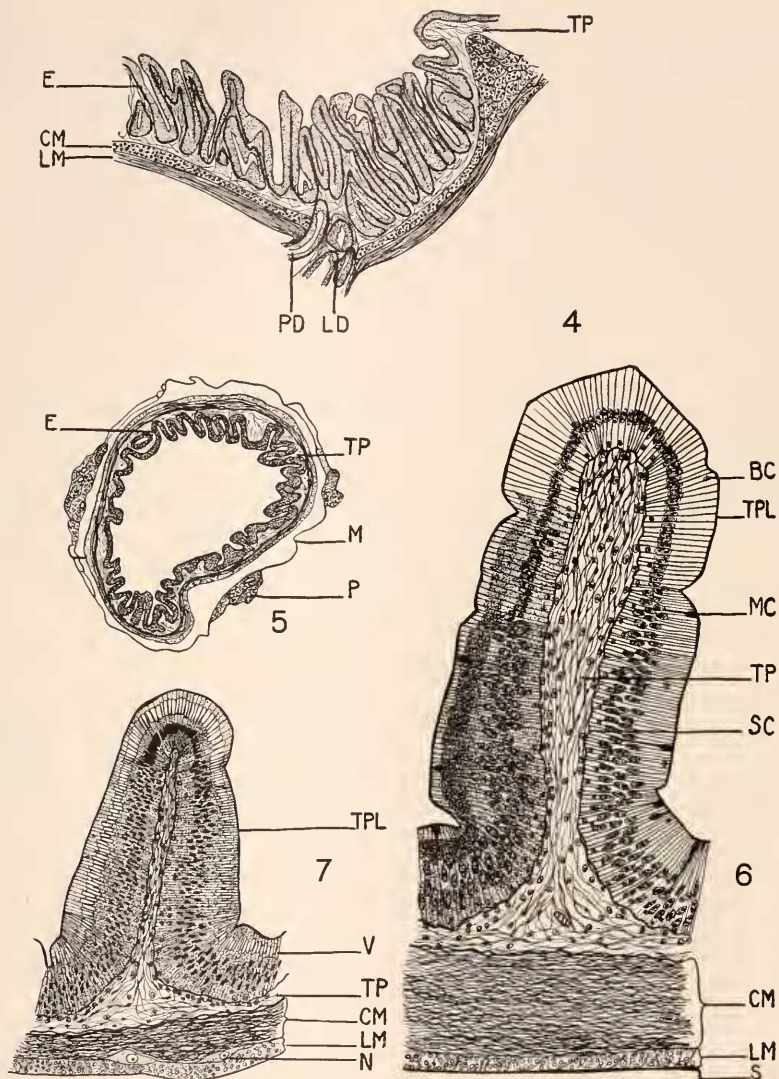
The dorsal diverticulum arose near the beginning of the oesophagus. It extended caudally and tapered to its junction with the pneumatic duct. The proximal portion of the diverticulum was lined with stratified epithelium continuous with that of the oesophagus (Fig. 2). The main part of the cavity was lined with simple columnar epithelium which did not appear to be of the secretory type. Cytoplasm of the cells was granular and the lightly staining nuclei were located toward the bases of the cells. The mucosa formed numerous small folds which lined branching evaginations of the main cavity. A few very short striated muscle fibers were present in the tunica propria. Two layers of muscle of equal thickness, an inner circular and outer longitudinal, comprised the muscular coat. These layers were relatively thin, consisted entirely of striated muscle and were directly continuous with the tunica muscularis of the oesophagus. The tunica serosa also continued from the oesophagus around the diverticulum.

Intestine

The mucosal folds in the entire intestine, viewed from the surface, followed a herringbone pattern. When the intestine was distended with food, these folds could be clearly seen through the walls. Sections showed that the folds of the intestinal bulb were higher and more complex than those of the intestine proper, often joining with each other above smaller folds (Fig. 4). The deeper portions thus appeared like glands and the folds, like villi. In the main part of the intestine, the folds were shorter and broader and exhibited a much simpler arrangement (Fig. 5). In the anal portion of the rectum, the mucosal folds became again very complicated and branching.

The epithelium of the intestine contained two types of cells, simple columnar and mucous. These cells were covered with a relatively thick top plate and were characteristically very long and narrow. There was, however, some variation in their height; at the apices of the folds they were slightly shorter while along the sides and in the deep portions of the folds, they were very tall. Nuclei of the columnar cells were usually located in the basal third of the cell and were broadly oval. In almost all of the nuclei clumps of chromatin were evident. The cytoplasm stained rather lightly, as a rule, although the cells covering the tips of the folds were considerably darker than the rest. The cytoplasm of all





(See p. 58 for abbreviations)

FIG. 4. Diagrammatic longitudinal section through the first part of the intestinal bulb showing entrance of ducts of the liver and pancreas. This shows the characteristic folding of the mucosa. The sphincter is at the extreme right. $\times 15$.

FIG. 5. Transverse section through the intestine proper showing type of mucosal folds. $\times 15$.

FIG. 6. Transverse section through a fold of the intestinal bulb showing, on one side of the fold, the details of structure of the epithelium. Note that the aggregation of cytoplasmic granules gives a banded appearance. Goblet cells are shown in solid black. $\times 175$.

FIG. 7. Transverse section through a fold of intestine showing vacuole in each cell. $\times 150$.

the cells was slightly granular. In most cases, in the first third or half of the intestine, the granulation appeared to be heaviest in the outer part of the cell and produced a banded effect in the epithelium. There was thus a distinct differentiation between the perinuclear cytoplasm and that in the outer part of the cell (Fig. 6).

In those fish which were killed immediately after feeding, there occurred a definite change in the epithelium in the last half of the intestine. Each cell contained a single vacuole immediately distal to the nucleus (Fig. 7). Cytoplasm was present between the vacuole and the luminal edge of the cell and the vacuoles, therefore, occupied a position in the cells corresponding to the location of heavy cytoplasmic granulation as it occurred in cells of the intestinal bulb and the first part of the intestine proper. In contrast to mucus, which occupied the entire distal end of a goblet cell and caused a distinct bulge in the wall, the vacuoles remained small and occupied a definitely limited area within each cell. They did not stain with any of the stains used but remained perfectly clear. The fact that they showed no reaction to mucicarmine indicated positively that the contents were not mucus. In fact, sections stained with Delafield's haematoxylin showed goblet cells filled with blue-staining mucus at the same time that vacuoles in the columnar cells remained unstained.

Mucous cells were very few in the intestine. The tips of the mucosal folds were generally entirely free of them; the greater number occurred in the deeper parts of the folds. They were about equally numerous in the intestinal bulb and in the intestine proper. They occurred singly and extended the entire width of the epithelium as typical goblet cells. The expanded portion of the cell was located usually at the luminal end but might occur anywhere between the top plate and the basement membrane. That part of the cell which was enlarged with mucus was typically spherical and the basal part containing the nucleus was long and filamentous. When the spherical portion was located below the distal end of the cell, the elongated slender part extended to the lumen (Fig. 6). The staining reactions of the goblet cells indicated that they were similar to the mucous cells of the pharynx and oesophagus.

The epithelium of the rectum resembled that of the oesophagus. Mucous cells were fewer and consequently less crowded, and individual cells in this region were the largest of any in the whole tract.

The tunica propria of the intestine was continuous with that of the oesophagus and formed a much more distinct layer. It was composed of areolar tissue containing fat cells. Mast cells occupied a more conspicuous place in the tissue than in the other parts of the tube, thus substantiating the results of Bolton (1933). A basement membrane was present and, directly beneath it, a few thickened fibers which might be

considered the stratum compactum although they did not form a conspicuous layer. Immediately above the muscle, however, was a definite sheet of tissue composed of large, wavy, collagenous fibers. This corresponded more closely in structure to the stratum compactum as figured by Rogick (1931) but its location would define it as submucosa. It arose quite definitely at the intestinal sphincter as a concentration of large longitudinal fibers.

The muscular coat was composed of two layers, an inner circular and an outer longitudinal. They were apparently not continuous with the tunica muscularis of the oesophagus and formed thinner sheets of tissue than in the more anterior parts of the tract (Fig. 5). The longitudinal fibers constituted a definite layer in contrast to the scattered fibers found more anteriorly. The fibers were striated throughout the greater part of the intestinal bulb and a few striated fibers extended into the intestine proper. Smooth muscle gradually replaced the striated and continued through the rectum. Nerve cells between the two muscle layers indicated the presence of a myenteric plexus. A typical serosa covered the entire intestine.

The bile duct and pancreatic duct entered the intestinal bulb a short distance caudal to the intestinal sphincter (Fig. 4). The epithelium of both ducts appeared stratified in some places. Actually, however, it was of the simple columnar type. The sub-epithelial connective tissue and a few striated muscle fibers were apparently continuous with similar tissues in the wall of the intestinal bulb.

DISCUSSION

The foregoing account furnishes a basis for comparison of the digestive tract of *Carassius* with that of other teleosts. In general structure, as well as in most of its details, it resembles closely the tract of the minnow, *Campostoma* (Rogick, 1931). Absence of a stomach suggests a certain similarity with the digestive tube of *Fundulus* but there are marked individual differences. The tract as a whole is considerably longer in *Carassius*, typically twice the body length, whereas in *Fundulus* the two are about equal. This is apparently the result of differences in length of the intestinal portion in the two species. Probably because of this, the intestinal bulb of *Carassius* is longer than the corresponding portion of the tract in *Fundulus* and not so sharply tapering. Variations in intestinal length in these three species may well be correlated with differences in diet. *Carassius* obviously represents an intermediate condition between the extremely long intestine of *Campostoma* and the short intestine of *Fundulus*.

Diversity in descriptive terminology presents difficulties in an exact comparison of the histological structure with the detailed accounts of the histology of the tract in other fishes. In general, however, there would seem to be a close correspondence among the several species which have been described. In particular, the epithelium of the pharynx and of the true intestine appears similar in *Carassius*, *Campostoma* (Rogick, 1931) and *Pleuronectes* (Dawes, 1929). Blake does not include a description of the pharynx in his account of *Centropristes* or *Prionotus* (1930, 1936). The oesophageal epithelium of these forms, however, is similar to that of *Carassius* and *Campostoma* and the similarity in structure of the intestine is striking.

The histological study is of particular significance in determining that at no point in the tract are there cells which resemble the cells of gastric epithelium. A special interest, therefore, attaches to the cells of the intestinal mucosa.

Both Rogick (1931) and Dawes (1929) describe in some detail the columnar cells of the intestinal epithelium. Dawes found that the resting cell contained a darkly-staining mass in the center. During active digestion, this mass disappeared but an area of darker cytoplasm appeared below a pale-staining border in each cell. The nuclei, likewise, exhibited differences in staining reaction under the two conditions. In her figure of the intestine, Rogick showed a clear area in approximately the middle of the cytoplasmic portion of each columnar cell. The darkly-staining cytoplasmic band and the clear area have been found in the intestinal epithelium of *Carassius*, the former in the intestinal bulb and upper intestine and the latter, in the lower part of the intestine proper. Rogick considers the clear vacuoles to be an early stage in the accumulation of mucus within the cell but the investigation on *Carassius* throws considerable doubt on this interpretation. In addition to the failure of these vacuoles to give the specific mucous reaction is the fact that no intermediate stages between these cells and typical goblet cells could be found. Moreover, no such vacuoles were found in cells of the pharynx and oesophagus where the mucous type was the most abundant. With one exception, vacuoles did not appear in the epithelium of fish which had been starved. This, coupled with the findings of Dawes, would indicate a possible relationship between the appearance of vacuoles and the presence of food in the alimentary tract. Unfortunately, no histological study accompanied the work of Babkin and Bowie (1928) on the physiology of digestion in *Fundulus*. Such a combined study would undoubtedly be of considerable value in determining the function of these cells.

SUMMARY

1. The digestive tube of *Carassius auratus* closely resembles that of *Campostoma anomalum* (Rafinesque).

2. Study of the gross structure brought out the following characteristics: the posterior pharynx possesses pharyngeal teeth which bite on a dorsal horny pad; a dorsal diverticulum leading to the pneumatic duct extends from the short oesophagus; the oesophagus opens directly into an expanded part of the intestine, the intestinal bulb; a circular sphincter marks the boundary between oesophagus and intestinal bulb; the intestine proper does not show the extreme coiling of *Campostoma* but is considerably longer than that of *Fundulus*; it leads into the rectum.

3. The walls of the entire tract possess a tunica mucosa, tunica muscularis and tunica serosa. Absence of a muscularis mucosae prevents the determination of a distinct submucosa.

4. Epithelium of the pharynx is stratified with numerous mucous cells in the superficial layer. At the intestinal sphincter, there is an abrupt change to the simple columnar epithelium of the intestine. Stratified epithelium with mucous cells appears again in the rectum.

5. Columnar cells of the intestinal bulb and upper intestine show a band of darkly-staining cytoplasm between the nucleus and the luminal edge of the cell. In the lower half of the intestine, this region of each columnar cell is marked by a single vacuole which does not react to any of the stains used.

6. The tunica propria of the posterior pharynx and oesophagus is invaded with muscle fibers from the muscular layer. It forms a distinct region in the intestine. A stratum compactum, while distinguishable, is not a conspicuous feature. Mast cells are present, particularly in the intestine.

7. Striated muscle forms the tunica muscularis of posterior pharynx, oesophagus and intestinal bulb. It is gradually replaced by smooth muscle in the intestine proper. Between the oesophagus and intestinal bulb, the circular layer of muscle becomes enlarged to form the intestinal sphincter.

8. A serosa covers the entire tract beyond the most posterior part of the pharynx.

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